VERNONIA (COMPOSITAE) IN THE BAHAMAS — REEXAMINED

STERLING C. KEELEY AND SAMUEL B. JONES, JR.

The flora of the Bahamas, as originially described by Britton and Millspaugh in 1920, included a large number of purportedly endemic species. However, in the early part of this century little was know of the causes or the extent of variation in natural populations; consequently some of the taxonomic treatments of that time were based on distinctions more apparent than real. Specific rank was often assigned on the basis of geographical location, particularly where islands were involved, rather than on any clear-cut morphological differences. Many of these species have since been shown to be insular representatives of mainland types and not truly endemic (Gillis 1974, 1975).

The treatment of *Vernonia* in Britton and Millspaugh (1920) was based on a paper by Gleason (1906) in which he distinguished several closely related taxa in sect. *Lepidaploa,* subsect. *Scorpidae* series *Reductae: V. arctata,* later synonymized to *V. arbuscula* Less. (Gleason 1922); *V. bahamensis* Griseb.; and *V. obcordata* Gleason. In the same paper, he also described a new species in subsect. *Paniculatae, V. insularis* Gleason.

Within series *Reductae* the three similar appearing taxa were distinguished primarily on the basis of leaf size and shape (Table 1). Gleason maintained that *Vernonia arbuscula* could be distinguished from *V. bahamensis* by its shorter broader leaves, more crowded branches and more numerous heads. The geographical distribution of these two species was reported to be non-overlapping, with *V. bahamensis* occurring in the more southerly islands. The third species, *V. obcordata,* was characterized by leaves as broad as long, obcordate at the apex, and a yellow pappus.

Vernonia insularis of subsect. *Paniculatae* was described from several of the northern islands. Due to the similarity in appearance between this species and *V. blodgettii* Small, an endemic of southern Florida, Gleason felt they were closely related. *Vernonia cinerea* (L.) Less., a pan tropical weed of sect. *Tephrodes,* was reported as introduced in New Providence (Gleason, 1906).

Table 1.

Characteristics used by Gleason (1906) to distinguish V. arbuscula, V. bahamensis and V. obcordata.

Character	V. arbuscula	V. bahamensis	V. obcordata
Leaf length, cm	1–1.8	2–3.5*	0.8–1.5
Leaf width, cm	0.6–1.1	0.5–1.2	0.7–1.5
Petiole length, mm	3–7	*	5
Involucre height, mm	4–5	3–4	4–5
Number of flowers per head	13	8–13	8–13
Achene length, mm	2.5	2–2.5	—
Inner pappus length, mm	5	4–5	—
Location:	New Providence Island	Fortune and Inagua Islands	Little Inagua Island

*Included in leaf length

Ekman (1914) examined the Bahaman Vernonias as part of his revision of the Vernonieae of the West Indies and accepted Gleason's treatment (1906) as substantially correct. Ekman pointed out that there was a close resemblance between *Vernonia arbuscula* and *V. bahamensis,* but he felt that the number of lateral veins in the leaves and the angle at which they issued from the main vein were sufficient to allow separation of these two taxa.

Since the early work by Gleason collections of Bahaman *Vernonia* have increased in number and encompassed more of the islands in the chain. Many of these specimens are difficult to identify using Gleason's criteria (Table 1), and have evidently been difficult to distinguish in the past. Many specimens have been annotated with at least two of the three possible specific epithets, and some have all three. In addition, the geographical distributions which in the past were used to separate the taxa, have become less distinct with the addition of new material, and these distinctions can no longer be used uncritically.

Geographical distribution strongly influenced taxonomic treatments in the early part of this century (Gillis 1974) and it is possible that the very similar appearing *Vernonia insularis* and *V. blodgettii* are actually conspecific, but this likelihood has not been examined. In short, the taxonomic status of these Vernonias is in need of review since the taxa are not well understood.

MATERIALS AND METHODS

Loans of herbarium material were obtained from US, NY, TEX, GH, MO, and F. Taxa were also grown and maintained in the greenhouse at UGA and used during this study for cytogenetic work and morphological comparisons.

Twenty-five specimens were selected from a group containing putative *Vernonia arbuscula, V. bahamensis,* and *V. obcordata* since many specimens have been annotated with at least two epithets. In addition, all specimens annotated by Gleason or identified by him in his 1906 paper were separated by species and scored. Each specimen was measured for the following characters: plant height, length and width of the leaf blade, ratio of length to width of the leaf blade, petiole length, involucre height, involucre width, inner phyllary length, inner phyllary width, number of flowers per head, number of achene ribs, achene length, inner and outer pappus length, corolla length and anther length. Midcauline leaves were selected for measurement on each specimen; only fully matured heads were used for measurements of length and width of involucres and phyllaries, anther length and corolla length were measured on soaked, fully mature flowers. Trichomes, venation patterns, and epidermal cell patterns were examined from leaves of herbarium material representing all taxa as annotated by Gleason. Trichomes were observed from leaf scrapings in aqueous mounts and on safranin stained leaf fragments cleared by the method of Herr (1971).

Field and greenhouse grown specimens of *Vernonia insularis* and *V. blodgettii* were measured and scored separately. Crosses were made between these two taxa by the method of Jones (1972), and the pollen of the progeny was examined for fertility by staining with aniline blue. Chromosome figures were examined from pollen mother cells of greenhouse grown *V. insularis, V. blodgettii* and their hybrid progeny, using the standard aceto-carmine staining technique. Trichomes, venation patterns, and epidermal cell patterns of leaves from greenhouse grown plants were examined and compared with herbarium material. Plastic nail polish impressions were made from fresh leaves. Leaves from herbarium specimens were cleared and stained. Leaves from greenhouse accessions of *V. insularis, V. blodgettii* and their hybrids were analyzed for sesquiterpene lactones by Dr. M. Betkowski at the University of Texas.

RESULTS AND DISCUSSION

Subsection Scorpidae Series Reductae:

Gleason reported the number of flowers per head in *Vernonia arbuscula* to be 13 (Table 1), however, counts of three heads per specimen on 13 sheets annotated by Gleason revealed a range of 9 to 14. Other key characters used by Gleason such as achene length, involucre height and inner pappus length were also found to be too variable and hence not useful in classification.

Although the branches were reported to be crowded in *Vernonia arbuscula,* and the heads more numerous than in *V. bahamensis* (Gleason, 1906), this character did not appear to be consistent. Some specimens obviously were taken from terminal branches; the number of heads in these terminal branches also appeared to be a variable character reflecting the length of time, and perhaps the availability of favorable growing conditions rather than any fixed and therefore measurable character of the taxon. Some specimens annotated by Gleason as *V. bahamensis* also had numerous, crowded heads.

Only one specimen of *Vernonia obcordata,* described by Gleason, was available and it was the holotype. Several sheets from later collections had prominently obcordate leaves. The pappus color, on the type specimen, and on other specimens with obcordate leaves was not particularly yellow as Gleason (1906) had indicated. During examination of soaked corollas, the pappus bristles of all taxa often turned yellow upon drying; it is possible that this was the source of the reported color variation.

Of the several characteristics originally used by Gleason to distinguish the three species in series *Reductae,* only leaf size and shape, and shape of the leaf apex correspondingly associated with distinct geographical distribution appeared to provide tentative criteria for positive identification. In attempting to faithfully apply these criteria, however, it soon became apparent that leaf size, at least, was too variable to be used. Gleason did not specify which leaves he scored, i.e. cauline or bracteal, and the range in size of leaves on one specimen alone was often great enough so that it could have been classified in all of the three possible taxa.

Five leaves were randomly selected from each specimen and were placed into one of the three categories of leaf shape given by Gleason (Figure 1, inset). This examination showed that leaf shape was also highly variable; and not geographically correlated (Figure 1). Of the 83 specimens examined, 43% had at least two leaf shapes and 18% had all three possible shapes.

A comparison of trichome complements revealed no differences between the taxa in this group. Uniserate, awl-shaped, awl-shaped glandular, L-shaped and T-shaped, glandular and non-glandular bilobed trichomes of Faust and Jones (1973) were observed. Stomata were found on both leaf surfaces. Venation patterns, reported to be distinctive by Ekman (1914), were found to vary with leaf size and were of little use in distinguishing taxa. The three taxa in the series *Reductae* should be reduced to a single variable taxon distributed throughout the Bahama Islands (Figure 2).

Subsection Paniculatae:

The means, standard deviations and range of representative morphological characteristics of field collected and greenhouse grown specimens of *Vernonia insularis* and *V. blodgettii* are shown in Figure 3. It is not possible to clearly differentiate field collected specimens of these two taxa on the basis of number of flowers per head, corolla length, anther length or involucre height and width. Although leaf size appears distinct in field collections, this difference is lessened when greenhouse grown specimens are included. This overlap indicates that leaf size is strongly influenced by environmental parameters and makes this character of dubious value for taxonomic determinations.

Vigorous and fertile first generation hybrids were produced from crosses between *Vernonia insularis* and *V. blodgettii* (Table 2). Examination of trichomes indicated that there were no consistent differences between parental accessions and/or their hybrids. Bilobed, awl-shaped glandular and L-shaped trichomes appeared in all specimens examined and stomata appeared on both leaf surfaces. No difference in epidermal cell size or shape, or venation patterns appeared in examinations of cleared leaf fragments from herbarium specimens.

Sesquiterpene lactone determinations indicated that *Vernonia insularis* contained glaucolide F and an unidentified sesquiterpene lactone, whereas *V. blodgettii* contained only glaucolide A. Glaucolides A and F differ by a single methyl group. Evaluation

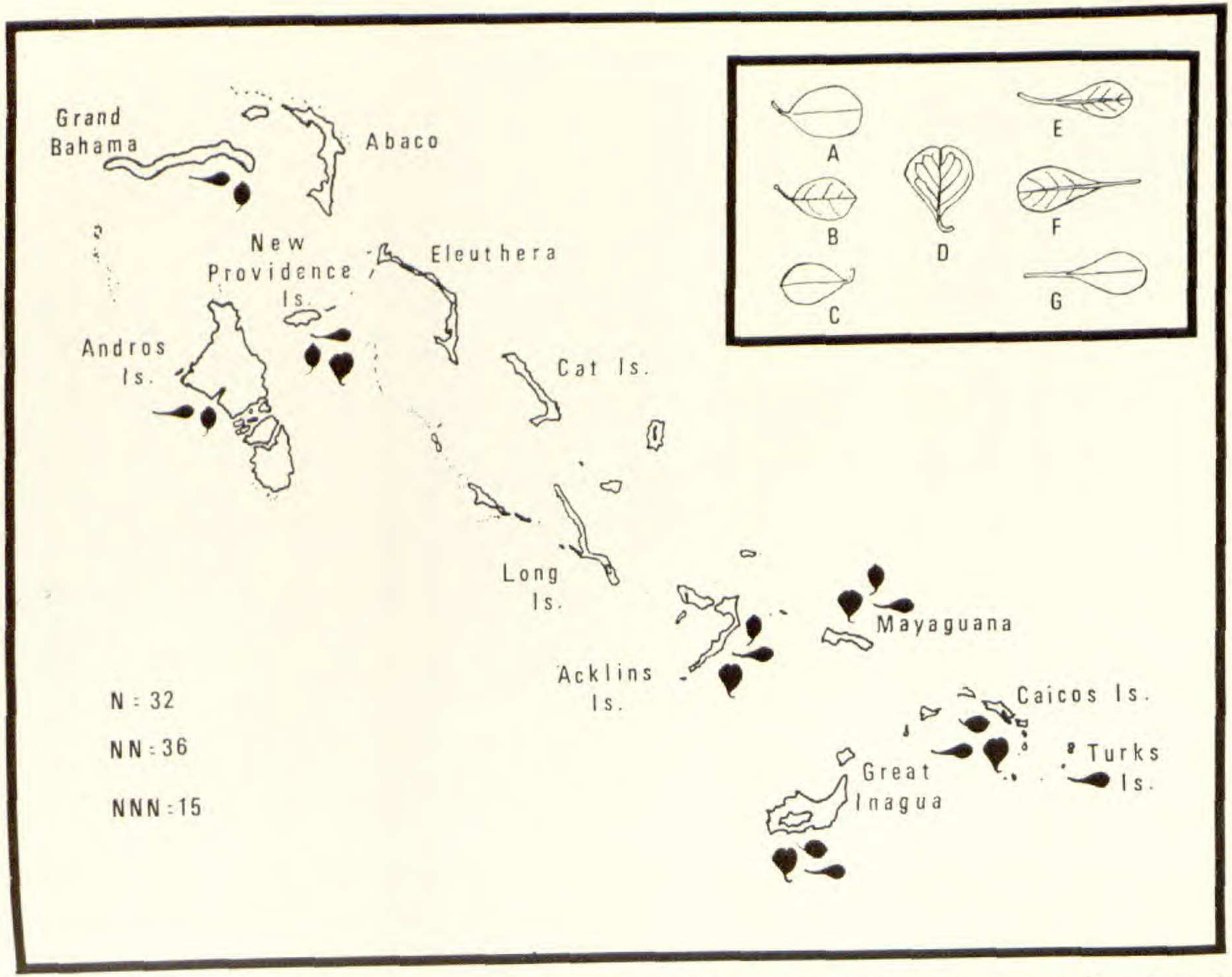

Figure 1 (inset). Leaf shapes used by Gleason to distinguish *Vernonia arctata* = *V. arbuscula* (A–C), *V. obcordata* (D), and *V. bahamensis* (E–G). Redrawn from Gleason (1906). The distribution of leaf type throughout the Bahama Islands for *Vernonia arbuscula* Less. N = the number of individuals with only one leaf shape, NN = the number of individuals with two leaf shapes and NNN = the number with all three leaf shapes.

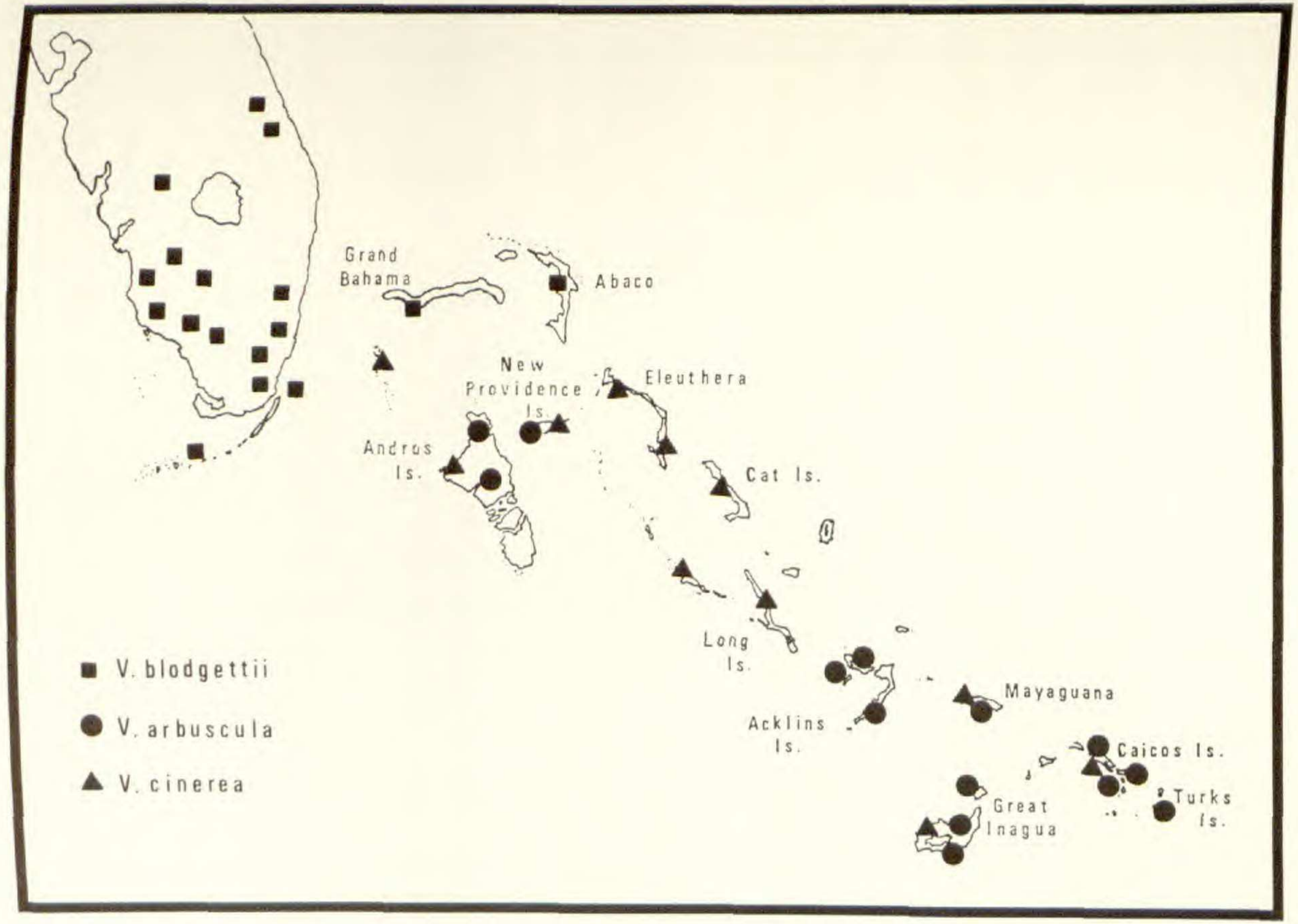

Figure 2. The distribution of *Vernonia blodgettii*, *V. arbuscula*, and *V. cinerea* in southern Florida and the Bahamas.

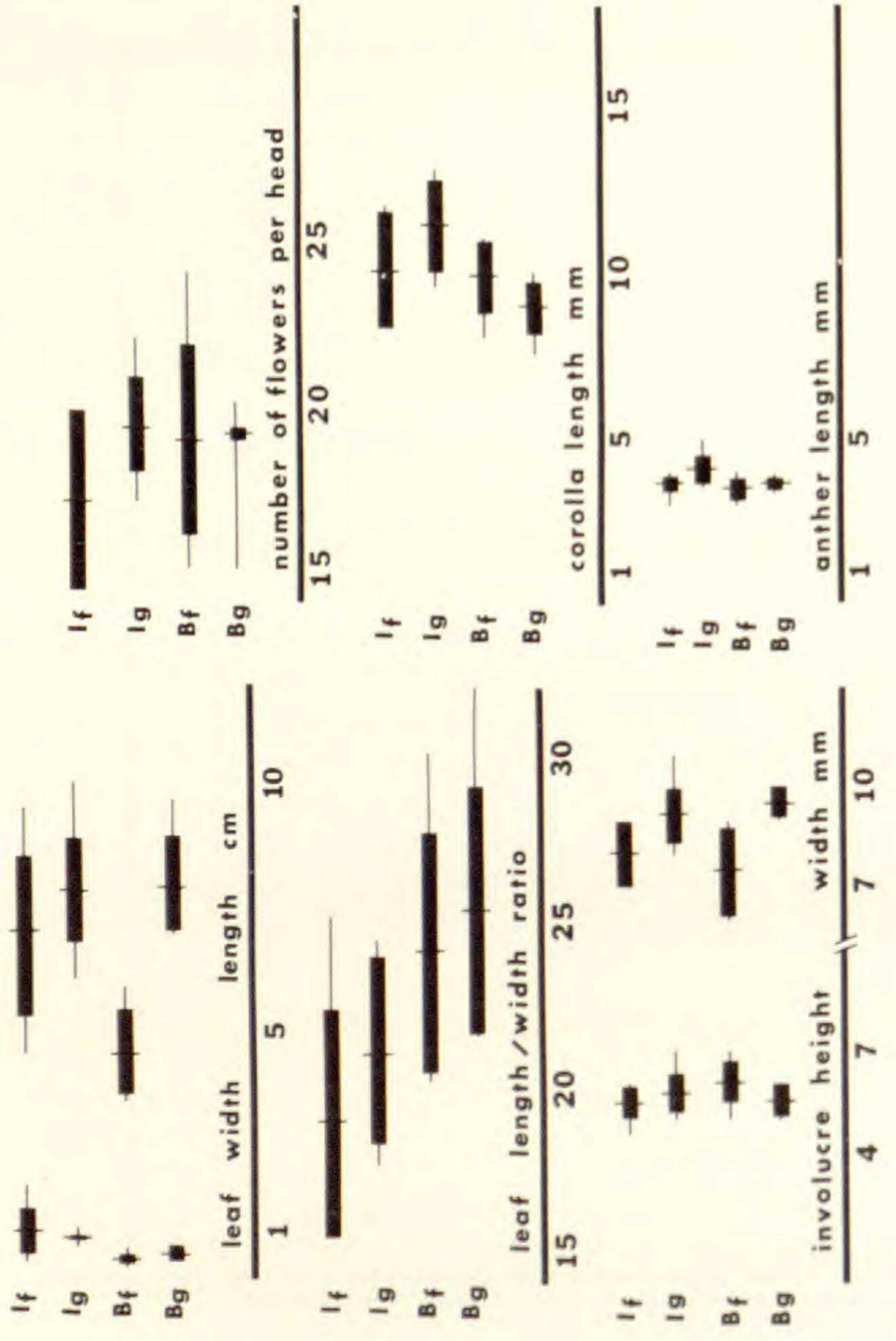

Figure 3. Selected morphological measurement of field collected *Vernonia insularis* (I_f), and greenhouse grown *V. insularis* (I_g), and field collected and greenhouse grown *V. blodgettii*, (B_f) and (B_g) respectively.

Table 2.

Summary of fertility in greenhouse accessions of V. insularis, V. blodgettii and their hybrids.

		Pollen Stainability	
Taxa	Generation	Range	Mean
V. blodgettii	P_1	55-89	69
V. insularis	P_1	(64)92-97	91
Crosses			
V. insularis × *V. blodgettii*	F_1	95	95*
V. blodgettii × *V. insularis*	F_1	93–100	94
		56-95**	88

* 1 count only.
**Second year.

of these differences is very difficult, however, since nothing is known of the extent of variation in sesquiterpene lactones within these taxa. Additionally, inheritance of sesquiterpene lactones is variable and is not well understood (Herout, 1970; Burnett, 1974). In any case it is difficult to provide a rationale for distinguishing macroscopic organisms on the basis of chemical differences that require special training and a sophisticated laboratory to detect (Davis & Heywood, 1963; Alston & Turner, 1972).

As pointed out by Gillis (1974) many species occurring in the Bahamas have been considered to be unique in the past because they were isolated from related mainland populations. This distinction may be valid if there are morphological differences which allow clear recognition of distinct taxa. However, when there are no morphological differences distinguishing the mainland groups from insular representatives there is little justification for maintaining separate taxonomic status, particularly when the individuals from each of the two areas are interfertile and produce viable and vigorous F_1 hybrid plants.

Dispersal and potential exchange of genes in nature has not been studied in these taxa; however, it cannot be overlooked. For example, the distance between Florida and the island of Abaco is scarcely 50 miles and well within the range of seed transport (Thorne, 1972). Thorne (1972) and McNeil and Burton (1973) have shown that wind and hurricanes, and bird migrations (which occur from Florida to the Bahamas) provide ready dispersal agents. If two mainland populations of a species were separated by this distance or a greater one, but were morphologically indistinguishable they would hardly be considered subspecies let alone distinct species. Recognition of disjunct species too, would scarcely be possible if geographical distance were taken as the main criteria for distinguishing species. Although the geographical range of this taxon includes an island, a separate specific designation would prejudge the evolutionary status and existence of a unique colonizing event by this taxon.

If systematists are to provide a working framework for biogeographers and others to use in understanding island floras, then perhaps the greatest service we can render is to avoid the historical pitfalls of island botanists and point out morphological and genetic similarity where it exists. To this end the following taxonomic revision is proposed:

KEY TO TAXA

a. Plants perennial.
  b. Fructicose to woody plants; flowers 8–12 per head; leaves 1–4 cm long, 0.82 cm wide. .... 1. *V. arbuscula* Less.
  b. Herbaceous plants; flowers 15–25 per head; leaves 6–10 cm long, 0.5–1 cm wide. .... 2. *V. blodgettii* Small.
a. Plants annual, flowers 12–16 per head; leaves 2–5 cm long, 1.5–2.5 cm wide. .... 3. *V. cinerea* (L.) Less.

1. **Vernonia arbuscula** Less., Linnaea **6:** 664. 1831. TYPE: **Mauritius** (error): *Salisbury 1816* (Holotype, destroyed at Berlin; neotype, here designated: **Bahamas,** near Nassau, *Curtiss 65* (US!)).

Vernonia arctata Gleason, Bull. Torrey Bot. Club **33:** 185. 1906. TYPE: **Bahamas:** near Nassau, New Providence, *Curtiss 65* (Isolectotypes: F! GH! US! MO!).
Vernonia obcordata Gleason, Bull. Torrey Bot. Club **33:** 187. 1906. TYPE: **Bahamas:** Inagua, *Nash & Taylor 1206* (Holotype: F!).
Vernonia bahamensis Griseb., Fl. Brit. W. Ind. 352. 1861. TYPE: **Bahamas:** *Brace 23/9/77* (Holotype: K!).
Cacalia bahamensis (Griseb.) Kuntze, Rev. Gen. 969. 1891.

Shrub up to 3 m tall; stems gray to brown tomentose, glandular dotted, often much branched at least terminally. Leaves crowded, especially on terminal branches, leaf blades 1.5–2(4) cm long, 0.6–1.5 (2.2) cm wide (length/width ratio ca. 1.5) widest above the middle, spatulate, obovate, obcordate, to lanceolate, surface gray-green tomentose, gland dotted, upper surface frequently darker than lower, often greener in appearance than lower surface which occasionally appears whitish. Leaves apically acute to blunt, retuse, emarginate to obcordate, basally tapering, margins entire to repand, petioles 6–8 mm long, grey-brown tomentose, glandular. Inflorescences much condensed on terminal cymes, usually with 3–5 heads. Heads 8–12 flowered, sessile, usually subtended by a small leaf. Involucres campanulate, 4–5 mm high, 4–5 mm wide; phyllaries tomentose to villous, closely appressed when immature, golden brown in color; inner phyllaries awl-shaped, tomentose to villous, with conspicuous resinous dots, 3.5–4 mm long, 1–1.5 mm wide, tips tapering, acute; outer phyllaries broadly awl-shaped, densely pubescent, size variable with age. Pappus whitish to straw colored; inner bristles 5–6 mm long, outer pappus scales 0.5–1 mm long, edges jagged often deeply cleft. Corollas 6–9 mm long, violet to rose-purple, smooth surface, little or no odor. Anthers (1.5) 2.5–3.2 mm long. Achenes 2–3.5 mm long, sericeous to hirsute, hairs shiny, 5–10 ribs 5 large, 10 smaller. $n = 17$. Flowering and fruiting all year.

This species is distributed throughout the Bahama Islands, in pinelands, and limestone barrens. It is a highly variable species, particularly with regard to leaf shape (Figure 1).

Ekman (1914) saw the original type specimen of *Vernonia arbuscula* during a visit to Berlin prior to 1914. He pointed out that it was the same as *V. arctata* Gleason and cited several specimens of *V. arctata* which he had seen; among these specimens was that of *Curtiss 65*. In 1922 Gleason reduced *V. arctata* to synonymy with *V. arbuscula*. Since Ekman had seen both Lessing's type of *V. arbuscula* and several specimens described by Gleason as *V. arctata* including *Curtiss 65*, it seems a logical choice for the Neotype.

REPRESENTATIVE SPECIMENS: **Bahamas:** Acklin's Island, *Brace 4330* (NY, US); Crooked Island, *Rothrock 276* (F); Mariguana, *Wilson 746* (NY, F, GH); Great Inagua, *Nash & Taylor 1017* (F, NY); Turks Islands, *Millspaugh & Millspaugh 9362* (F, NY, GH); Caicos, *Wilson 7721* (NY, F); New Providence, *Wight 70* (NY, F, GH); Andros, *Brace 6926* (F, NY); Castle Island, *Wilson 7783* (NY, F, GH); Fortune Island, *Eggers 3832* (NY, US).

2. **Vernonia blodgettii** Small, Fl. S. E. U. S. 1160. 1903. TYPE: **Florida:** Pine Key, Monroe County, *Blodgett* (Holotype: NY!).

Vernonia angustifolia Michx. var. *pumila* Chapm., Bot. Gaz. 3: 5. 1878. TYPE: same as for *Vernonia blodgettii*.

Vernonia insularis Gleason, Bull. Torrey Bot. Club **33:** 184. 1906. TYPE: **Bahamas:** Great Bahama, *Britton & Millspaugh 2392* (Holotype: NY!).

Stems erect, glabrous, often branches at base, 2–5 dm tall. Leaves mostly basal, 1.8–6.9 cm long, 0.1–1.0 cm wide, linear or nearly so, glabrous above, lightly glandular dotted below, tips obtuse to acute, attenuate at the base, margins slightly revolute, entire. Inflorescence loose, irregular, with few heads. Heads about 21-flowered. Involucre loosely and irregularly imbricated, campanulate, 5–8.5 mm high, 5.5–10.5 mm wide. Bracts deltoid to lanceolate, inner 3.9–6.7 mm long, outer 1.7–3.5 mm long, purple, glabrous to slightly pubescent. Bract tips acute to subacute, 0.1–0.5 mm long. Achenes pubescent, ribbed, 2.3–2.7 mm long. Pappus light yellow, bristles 5.5–7.8 mm long, scales irregular, 0.5–0.8 mm long. $n = 17$.

REPRESENTATIVE SPECIMENS: **Bahamas:** Abaco: *Gillis 7737* (GA), *Robertson 330* (GH); *Proctor 3043* (TEX); *Brace 1835* (NY); Grand Bahama: *Brace 3683* (F, NY); *Britton & Millspaugh 2392* (NY). **Florida:** Indian River Co.; *Small 8882* (NY); Brower Co. *Small 1634* (NY); Charlotte Co.; *Jones 1101* (GA). For a complete list of Florida localities see Jones (1964a).

3. **Vernonia cinerea** (L.) Less., Linnaea **4:** 291. 1829. TYPE: No location given (LINN, IDC microfiche!).

Conyza cinerea L., Sp. Pl. 862. 1753.
Cacalia cinerea (L.) Kuntze, Rev. Gen. Pl. 323. 1891.
Seneciodes cinereum (L.) Kuntze ex Post & Kuntze, Lex. Gen. Phan. 515. 1904.

Annual; stems tomentulose with T-shaped hairs sometimes becoming glabrate with age below and tomentulose with T-shaped hairs above, 3–6 dm high; leaves scattered along stem; blades of middle stem leaf 1.5–2.5 cm wide, 2–5 cm long, lanceolate, pubescent above, pubescent with T-shaped hairs, and punctate beneath, apically acute, basally attenuate, margins remotely toothed; petioles margined, ca. 1.5–2.5 cm long, pubescent; inflorescence loose, open and often spreading; heads 12–16 flowered; involucre campanulate, 6–7 mm high, 5–6 mm wide; phyllaries loosely and irregularly imbricate; inner phyllaries linear-oblong, 5–5.5 mm long, 0.6–0.8 mm wide, with acuminate to subulate purplish tips 0.5–1 mm long; pappus whitish, deciduous; inner bristles ca. 4 mm long; outer bristles ca. 0.2 mm long; corollas purplish-lavender, 6–7 mm long; achenes rounded, nearly ribless, ca. 1.5 mm long; flowering the year around. $n = 9$.

LITERATURE CITED

ABDEL-BASET, Z. M. 1973. Biochemical systematic investigations of western hemisphere species of genus *Vernonia* (Compositae) emphasizing flavonoid chemistry. Ph.D. Dissertation, Univ. Texas, Austin. 161 pp.

ALSTON, R., & B. L. TURNER. 1959. Segregation and recombination of chemical constituents in a hybrid swarm of *Baptisia laevicaulis* × *B. virifis* and their taxonomic implications. Am. Jour. Bot. **46:** 678–686.

BRITTON, N. L., & C. F. MILLSPAUGH. 1920. Bahama flora. New York, Hafner Pub. Co. 695 pp. Reprinted 1962.

BURNETT, W. C., JR. 1974. Sesquiterpene lactones — herbivore feeding deterrents in *Vernonia* (Compositae). Ph.D. Dissertation. University of Georgia, Athens, Georgia. 322 pp.

DAVIS, P. H., & V. H. HEYWOOD. 1963. Principles of angiosperm taxonomy. London, Oliver and Boyd Ltd. 558 pp.

EKMAN, E. L. 1914. West Indian Vernonieae. Uppsala. Almquist & Wiksells. 106 pp.

FAUST, W. Z., & S. B. JONES, JR. 1973. The systematic value of trichome complements in a North American group of *Vernonia* (Compositae). Rhodora **75:** 517–528.

GILLIS, W. T. 1974. Phantoms in the flora of the Bahamas. Phytologia **29:** 154–166.

———, & G. R. PROCTOR. 1975. Additions and corrections to the Bahama flora. II. Sida **6:** 52–62.

GLEASON, H. A. 1906. The genus *Vernonia* in the Bahamas. Bull. Torrey Bot. Club **33:** 183–188.

———. 1922. Vernonieae. N. Am. Fl. **33:** 52–95.

HERR, J. M., JR. 1971. A new clearing-squash technique for the study of ovule development in angiosperms. Am. Jour. Bot. **58:** 785–790.

HEROUT, V. 1970. Chemotaxonomy of the family Compositae (Asteraceae). Pp. 93–110 in: WAGNER, H. & L. HÖRHAMMER. Pharmacognosy and phytochemistry. Springer-Verlag, Berlin.

JONES, S. B., JR. 1964a. Taxonomy of the narrow-leaved *Vernonia* of the southeastern United States. Ph.D. Dissertation. University of Georgia, Athens, Georgia. 182 pp.

———. 1964b. Taxonomy of the narrow-leaved *Vernonia* of the southeastern United States. Rhodora **66:** 382–401.

———. 1972. A systematic study of the Fasciculatae group of *Vernonia* (Compositae). Brittonia **24:** 28–45.

MCNEIL, R., & J. BURTON. 1973. Dispersal of some southbound migrating North American shorebirds away from the Magdalen Islands, Gulf of St. Lawrence, and Sable Island, Nova Scotia. Carib. Jour. Sci. **13:** 257–278.

THORNE, R. F. 1972. Major disjunctions in the geographical ranges of seed plants. Quart. Rev. Biol. **47:** 365–411.

DEPARTMENT OF BOTANY
UNIVERSITY OF GEORGIA
ATHENS, GEORGIA 30602